Green Turtle Grazing:
Effects on Structure and Productivity in Seagrass Ecosystems

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OBJECTIVES

1. Evaluate effects of simulated green turtle grazing, as well as the rate and extent of recovery after cessation of grazing, on various parameters in a Caribbean seagrass (*Thalassia testudinum*) bed, including:
   - Seagrass standing crop and physical structure (blade length and width, shoot density, number of blades per shoot, detrital layer thickness)
   - Seagrass productivity (areal growth, mass growth, productivity:biomass ratios)
   - Seagrass blade nutrient composition (organic matter, energy, nitrogen, phosphorus, fiber)
   - Seagrass rhizome biomass and nutrient composition (organic matter, nitrogen, phosphorus, fiber)
   - Sediment particle size and organic matter content

2. Improve estimates of carrying capacity of *T. testudinum* for green turtles by incorporating changes in *T. testudinum* productivity and nutrient content due to green turtle grazing.

BACKGROUND

Structure, Function, and Productivity of *T. testudinum* Ecosystems

Seagrass pastures, particularly of *T. testudinum* or turtle grass, form the basis of a major marine ecosystem in South Florida and the Greater Caribbean (Zieman 1982). Seagrass ecosystems are recognized as extremely productive systems that support a diverse array of life forms, including many species of economic importance. Considerable efforts have been invested in conserving and restoring seagrass pastures in South Florida.

The green turtle, *Chelonia mydas*, is the only herbivorous sea turtle and, in the Greater Caribbean including the South Florida region, feeds primarily on a diet of *T. testudinum* (Bjorndal 1997). Green turtle populations in the Greater Caribbean and Florida have been drastically reduced as a result of over-exploitation by humans over the past few centuries (Parsons 1962) and perhaps even before that (Jackson et al. 2001). Recent estimates suggest current green turtle populations may represent only 3-7% of past numbers (Jackson et al. 2001). This extirpation of the major seagrass herbivore has undoubtedly had major effects on the structure, function, and productivity of seagrass ecosystems (Bjorndal 1980, 1985, Ogden 1980, Thayer et al. 1982, 1984, Jackson 1997).

Because of the characteristics of herbivore populations in general and green turtles in particular, it has been assumed that under natural conditions, green turtle populations are limited by food resources (Bjorndal 1982, Jackson 1997). Thus, in the past, *T. testudinum* pastures were grazed to a much greater extent than they are today. Green turtles have a specific grazing pattern. They do not graze randomly throughout *T. testudinum* pastures; rather, green turtles maintain grazing plots by re-cropping grazed areas at as little as 4 to 10 day intervals (Bjorndal 1980, Ogden 1980, Ogden et al. 1983). These plots vary in size and can be maintained for at least a year (Ogden 1980). Where green turtle populations are more dense and/or the *T. testudinum* stands are more sparse, grazing plots can merge so that entire *T. testudinum* pastures are grazed (Williams 1988). Based on studies in Jamaica (Greenway 1974) and St. Croix

(Zieman et al. 1984), it appears that after approximately one year of repeated clipping (simulating green turtle grazing), productivity of *T. testudinum* plants declines and blade width decreases, presumably in response to depletion of rhizome nutrient stores. During the first year of a grazing plot, green turtles ingest a higher quality, more digestible diet by grazing on the young growth in the grazing plots (Bjorndal 1980, Zieman et al. 1984). The effect of repeated clipping for more than one year on the nutrient composition of *T. testudinum* blades and thus on the quality of the diet of the green turtle, is not known.

Therefore, the *T. testudinum* ecosystems that marine ecologists have studied over the last few decades – characterized by high productivity, long leaf blades with heavy loads of epibionts that provide shelter to a diverse array of organisms and function as an effective baffle to trap detritus – may be a fairly recent phenomenon. When grazed by natural levels of green turtles, *T. testudinum* pastures are probably characterized by different productivity levels, blades a few cm in length that do not have time to acquire heavy loads of epibionts and that do not provide the structure or baffling effects of modern-day *T. testudinum* beds. Clearly, the structure, functions, and productivity of *T. testudinum* ecosystems are substantially different as a result of the population declines of the green turtle.

<u>Carrying Capacity of *T. testudinum* Pastures for the Green Turtle</u>

One of the problems we face in recovering populations of endangered species is identifying the desired population level to use as a goal. How many green turtles used to inhabit the Greater Caribbean and the waters of South Florida? What density of green turtles are required to fulfill their natural role in the ecosystem? Jackson (1997) discussed the challenge of assessing population declines when the true population's baseline is not known (the "shifting baseline syndrome"; Pauly 1995), and he used an estimate of carrying capacity (Bjorndal 1982) to calculate pre-Columbian green turtle population levels in the Greater Caribbean.

Bjorndal (1982) calculated a carrying capacity of *T. testudinum* for green turtles based on estimates of *T. testudinum* productivity and rates of food intake in green turtles. As she pointed out, a limitation in her estimation was the extent to which carrying capacity of *T. testudinum* would decrease as a result of productivity decline and perhaps nutrient quality decline under continual grazing. Also, her calculation of carrying capacity was based on the energy requirements of adult female green turtles; the estimate would be improved by incorporating adult males and immature size classes. We now have good baseline data on green turtle growth rates (Bjorndal and Bolten 1988, 1995, Bjorndal et al. 2000) and can construct reasonable size class structures for green turtle populations. In addition, recent analyses of green turtle growth rates have revealed a density-dependent effect (Bjorndal et al. 2000). Such density-dependent effects should be incorporated into the estimate of carrying capacity.

Our ability to estimate pre-historic green turtle populations would be greatly improved if we could incorporate realistic estimates of decreased *T. testudinum* productivity and/or decreased nutrient quality in response to extensive grazing into estimates of carrying capacity.

METHODS

Study Site

- Field work was conducted at Caribbean Marine Research Center on Lee Stocking Island, Exuma Cays, Bahamas
- Site was a contiguous, monospecific stand of *Thalassia testudinum* at 4 m depth
- Thirty square 9 m^2 plots (15 experimental, 15 control) were established in July 1999
- Plots were arranged in three sets of 10 (5 experimental, 5 control) within the seagrass bed; within each plot, experimental and control plots were alternated and were all 4 m away from each other
- Rhizomes around the edges of each experimental plot were severed to a depth of ~35 cm with a flat-bladed shovel every 6-8 weeks to prevent nutrient translocation along rhizomes from adjacent unclipped grass

Clipping Maintenance

- Clipping was maintained in 15 experimental plots from July 1999 to November 2000
- All blades in each plot were initially clipped to a height just above the blade/sheath junction (~2 cm above sediment)
- Blades from inner 4 m^2 area were collected, rinsed, dried to a constant weight at 60^o C, and weighed
- Each plot was re-clipped every time mean blade length reached 5 cm above the point of clipping, simulating bite size of a foraging green turtle (Williams 1988)

Sampling

Productivity

- Linear growth rates (cm/day) were measured in 30 blades in each experimental plot prior to each clipping
- Linear growth of 30 blades was measured in each control plot every 2 weeks using a basic staple technique (Zieman 1974)
- Because of physical changes in *T. testudinum* structure, areal growth rates (mm^2/day) were also calculated by incorporating blade width into the equation
- Growth was also quantified in terms of biomass (g/m^2) using weights of dried *T. testudinum* blades collected from experimental plots at each clipping and from control plots at sampling intervals
- Ratios of aboveground productivity ($g\ m^{-2}\ day^{-1}$) to aboveground biomass ($g\ m^{-2}$) were calculated for all plots

Physical Structure

- Physical structure was measured in both experimental and control plots every 2 weeks
- Blade length (cm) and width (mm) of 30 blades were measured
- Number of blades per shoot, shoot density (shoots/m^2), and thickness of the detrital layer (cm) were quantified in three 0.0625 m^2 quadrats

Blades, Rhizomes, and Sediment

- *Thalassia testudinum* blades and rhizomes, and sediment were sampled prior to clipping initiation and again at four intervals during clipping (2, 6, 11, and 16 months)

- Blades were collected from three 0.0625 m^2 quadrats in each control plot, rinsed, and dried to a constant weight at 60^o C
- Rhizomes were collected from one 1140 cm^3 core in each plot, separated by hand from surrounding sediment, and dried to a constant weight at 60^o C
- Sediment was collected from three 304 cm^3 cores in each plot and dried to a constant weight at 60^o C, after removal of invertebrates and vegetation that were visible to the naked eye

Effects of Season of Clipping Initiation

- Five new experimental plots were established within the *T. testudinum* bed in February 2000 to determine the role that season of clipping initiation plays in the response of the seagrass community to clipping
- Clipping was maintained from February to December 2000 under the same regime as the original 15 plots
- Physical structure and growth measurements were made in these plots at the same intervals
- Blades from each clipping were also dried for productivity and nutrient analyses, but sediment samples were not taken

Plot Recovery

- Experimental and control plots were sampled again in June and October 2001
- Physical structure was measured and *T. testudinum* blades were collected at both intervals, and rhizomes were collected in October only
- Sediment was not re-sampled during these recovery trips

Nutrient and Energy Determinations

- Blades and rhizomes were ground to pass through a 1-mm screen in a Wiley mill
- Dry matter content of blades and rhizomes was determined by drying for 16 h at 105^o C
- Organic matter content was determined by combustion at 500^o C for 3 h in a muffle furnace
- Energy and nutrient content of blades and rhizomes were calculated on dry matter and organic matter bases
- Energy content (of blades only) was determined using a Parr oxygen bomb calorimeter (Parr 1960)
- Nitrogen and phosphorus analyses were performed using a modification of the aluminum block digestion procedure (Gallaher et al. 1975); nitrogen and phosphorus content of the digestate were determined by semi-automated colorimetry (Hambleton 1977)
- In vitro organic matter digestibility (IVOMD) (of blades only) was determined by a modification of the two-stage technique (Moore and Mott 1974)
- Cell contents were removed from blade and rhizome samples using neutral detergent solution; remaining sample was called neutral detergent fiber (NDF) (Van Soest and Wine 1967)
- Hemicellulose was removed from samples using acid detergent solution; remaining sample was called acid detergent fiber (ADF) (Van Soest 1963)

- NDF and ADF content were determined in the Ankom^{200} Fiber Analyzer (Ankom Technology 1998, 1999)
- Cellulose was removed from samples with sulfuric acid, using the acid detergent lignin technique (Van Soest 1963)
- Lignin was removed (from blade samples only) with potassium permanganate solution (Van Soest and Wine 1967)
- Cutin fraction (of blade samples) was determined, after combustion at 500^o C for 3 h in a muffle furnace, as remaining organic matter after lignin removal

Sediment Analyses

- Sediment was ground with a mortar and pestle to pass through a 1-mm screen
- Dry matter content was determined by drying for 16 h at 105^o C
- Organic matter content was determined by combustion at 500^o C for 3 h in a muffle furnace
- Organic carbon content was determined using a modification of the chromic acid titration method (Walkley and Black 1934)
- Particle size (% sand, silt, and clay) was determined using a 0.063 mm sieve and a modification of the hydrometer technique (Buoyoucus 1936, Day 1965, Gee and Bauder 1986)

Data Analyses

- Differences in all parameters between experimental and control treatments over time were determined with a two-factor Repeated Measures ANOVA and individual t-tests using the Statistical Package for the Social Sciences (SPSS) version 10.0
- In the Repeated Measures ANOVA, time was the within-subject factor and treatment (clipped vs. unclipped plots) was the between-subject factor
- Percentages were arcsine transformed before analysis
- Differences were considered significant at the $\alpha = 0.05$ level

RESULTS

Productivity

- Growth rates of *T. testudinum* in both the control and experimental treatments were highly influenced by seasonal variation, resulting in higher growth during the summer seasons
- Areal growth in experimental and control plots was not significantly different; there did not seem to be any appreciable drop-off in productivity, even after the experimental plots were clipped for 16 months
- In terms of biomass, productivity of experimental plots also tracked that of control plots
- Productivity:biomass ratios in experimental plots were significantly higher than in control plots for the duration of the clipping experiment

Physical Structure

- Blade lengths in experimental plots became significantly shorter than in control plots due to the clipping treatment; 6 months post-clipping, blade lengths were still significantly

shorter, but by 11 months post-clipping, blade lengths were no longer significantly different in experimental and control plots
- Blade widths in experimental plots decreased significantly in response to clipping; widths were still significantly narrower as long as 11 months post-clipping
- The thickness of the detrital layer decreased significantly in experimental plots after almost a year of clipping; the experimental detrital layer was still thinner at 6 months post-clipping, but after 11 months, there was no significant different between the two treatments
- The number of blades per shoot decreased slightly in experimental plots toward the end of the clipping treatment, and was still significantly lower in experimental plots at 6 months post-clipping, but was not significantly different from control plots by 11 months post-clipping
- Shoot density in experimental and control plots was not significantly different during clipping, although there was a trend toward decreased shoot density in experimental plots; shoot density actually was significantly lower in experimental plots at 6 months post clipping, but there was no difference between treatments after 11 months
- Blade biomass was significantly lower in experimental plots due to clipping; this difference was still significant 6 months after clipping, but by 11 months post-clipping, there was no difference between the control and experimental plots
- Rhizome biomass was not significantly different between the two treatments at any point during clipping

<u>Nutrient Content</u>

- Blade organic matter content increased significantly due to clipping and was still higher after 6 months post-clipping; after 11 months, there was no difference between the two treatments
- Blade energy content increased significantly in experimental plots and did not return to levels found in control plots until 11 months post-clipping
- Blade nitrogen content increased significantly in experimental plots and did not return to levels found in control plots until 11 months post-clipping
- Blade phosphorus content increased significantly in experimental plots and did not return to levels found in control plots until 6 months post-clipping
- Blade NDF, ADF, lignin, and cutin content increased significantly in experimental plots and did not return to levels found in control plots until 11 months post-clipping
- Blade cellulose content increased significantly in experimental plots but at 6 months post-clipping was not significantly different from levels in control plots
- Blade IVOMD was marginally significantly ($p=0.047$) lower in experimental plots only in June 2000, 11 months after initiation of clipping
- Rhizome organic matter content significantly decreased in experimental plots due to clipping, but there was no longer any difference between treatments at 11 months post-clipping
- Rhizome nitrogen content significantly decreased in experimental plots, but there was no longer any difference between treatments at 11 months post-clipping
- Rhizome phosphorus content did not differ between the two treatments at any point during clipping

- Rhizome NDF, ADF, or lignin content did not differ between the two treatments at any point during clipping

Sediment

- Percent sand, silt, and clay were not significantly different between experimental and control plots at any point during clipping; therefore, sediment was not sampled on the two recovery trips
- Organic matter content was not significantly different between treatments at any point during clipping
- Organic carbon content in experimental plots was marginally significantly lower than in control plots only in June 2000, 11 months after initiation of clipping

Effects of Season of Clipping Initiation

- This component of the study is still being analyzed and will be discussed completely both in Kathleen Moran's PhD dissertation and in a manuscript stemming from that dissertation, which will be submitted for publication to Ecological Monographs

CONCLUSIONS

- Simulated grazing did significantly affect physical structure of the seagrass by decreasing blade length and width, detrital layer, blades/shoot and aboveground biomass; green turtles have a significant physical effect on their foraging grounds, which may also have an impact on other faunal components of the seagrass community, such as epibionts or sediment infauna
- Clipped seagrass blades also contained a higher energy and nutrient content than unclipped seagrass during the course of the experiment; by grazing in the manner that they do, turtles improve the quality of their food source for themselves by increasing the nutritive value of seagrass, which would induce them to continue grazing in the same plots, instead of moving on to new ungrazed grass
- Contrary to existing ideas that green turtle grazing initially stimulates and then dramatically decreases seagrass growth rates, simulated grazing in this experiment did not result in such an effect on seagrass growth; we found that the clipped seagrass plots maintained levels of productivity comparable to unclipped grass, which again plays a role in the maintenance of long-term grazing areas for green turtles
- Productivity:biomass ratios are measures of how much seagrass material is being produced relative to the amount of seagrass material in an area; because ratios were so much higher in experimental plots, this suggests that seagrass beds full of foraging turtles would be able to sustain a higher relative level of productivity than seagrass beds that are currently depleted of most of their megavertebrate grazers
- Seagrass beds recover relatively quickly after cessation of simulated grazing; therefore, today's seagrass may be able to support many more green turtles than we previously believed
- Estimates of green turtle carrying capacity for Florida, the Bahamas, and the Greater Caribbean are still to be determined and will be improved over previous estimates as a result of this project

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